Salience maps in parietal cortex: Imaging and computational modeling

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A B S T R A C T

Models of spatial attention are often based on the concept of a salience map. In computational cognitive neuroscience, such maps are implemented as a collection of nodes with self-excitation and lateral inhibition between all nodes (competitive interaction map). Here, we test some critical predictions of this idea. We argued that task demands, more precisely the level of attention required, can top-down modulate the level of lateral inhibition in a salience map, and thus induce different activation functions. We first show that a model with a high lateral inhibition parameter generates a monotonous activation curve as a function of set size similar to that typically observed in the literature (e.g. Todd and Marois, 2004). Next, we show that a competitive interaction map with medium lateral inhibition leads to a A-shaped activation curve when set sizes increase. This prediction is confirmed in an fMRI experiment with medium attention demands where a similar A-shaped activation curve is found in a posterior superior parietal area that was proposed to house a salience map (Todd and Marois, 2004). Finally, we show that a qualitatively different V-shaped activation curve is predicted with a very low inhibition parameter. An fMRI experiment with low attentional demands revealed this V-shaped activation curve in the same region. These findings provide critical support for the existence of a salience map based on competitive interactions in posterior superior parietal cortex, and suggest that its parameters (in particular, lateral inhibition) can be modulated in a top down manner dependent on task demands.

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stimuli in these studies were not controlled for non-numerical parameters (e.g. total luminance and item size), which co-vary with the set size and hence could be confounds in the reported activations.

These drawbacks were taken care of in a study by Santens et al. (2010). In that study, subjects were asked to estimate the number of items (i.e. set size) presented simultaneously in each display, which varied from one to five. For this task, subjects need to determine the position of the items in order to find out how many there are. Hence, the items must be represented in the salience map. Importantly, the items did not differ in any other way; hence no encoding of other features was possible. The authors also controlled their stimuli carefully for non-numerical parameters. The finding of increasing activation with an increasing set size in the same parietal area as stimuli in these studies were not controlled for non-numerical parameters (e.g. total luminance and item size), which co-vary with the set size and hence could be confounds in the reported activations.

reported by Todd and Marois (2004) then suggests that this activation with an increasing set size in the same parietal area as stimuli in these studies were not controlled for non-numerical parameters. The active maintenance mechanism implemented as recurrent self-maintained simultaneously, but this is accompanied with a cost in the visual field. Consequently, more than four elements can be maintained simultaneously, but this is accompanied with a cost in the quality of the representation. A third perspective on the capacity limit can be obtained from computational studies in which working memory is typically modeled as a salience map consisting of a collection of nodes. Each node corresponds to a neuronal population coding for a given location in space. This model is equipped with an active maintenance mechanism implemented as recurrent self-excitation of the nodes (e.g. Grossberg, 1980; Usher and Cohen, 1999; Wong and Wang, 2006). In addition, lateral inhibition between the nodes is implemented to reduce noise in randomly activated nodes (e.g. Gutkin and Smith, 2000). This leads to competitive interactions between the nodes in the map (Deco and Rolls, 2005; Rolls and Deco, 2006). With an appropriate balance between recurrent excitation and lateral inhibition a stable encoding of spatial structure of the visual display can be created. The implementation of lateral inhibition in working memory models leads to a capacity limit of the map. In particular, the activation of the map reaches a peak at a fixed set size (e.g. four) and decreases for larger set sizes (leading to loss of information). This is because the total amount of inhibition between the nodes in the map increases with the number of active nodes. As a consequence, the total activation in the map is limited. Hence, although there is no fixed capacity limit in this perspective, we may loosely think of the set size at which peak activity is obtained as a type of capacity limit. Interestingly, different settings of the lateral inhibition parameter lead to different set sizes where peak activation is reached.

Furthermore, the inhibition parameter functionally defines a threshold for neurons to become activated by input. If the threshold (inhibition parameter) is too low, neurons can be activated by random noise. On the other hand, if the inhibition parameter is too high, genuinely active neurons will be inhibited. Hence, a high level of lateral inhibition leads to precise representations (no noise), but also to a small capacity of the map. Lower levels of lateral inhibition leads to coarser representations (nodes activated by noise), but more items can be stored.

It is known that top down attention is able to bias competitive interactions in visual areas and beyond (Deco and Rolls, 2005; Reynolds et al., 1999; Rees et al., 1997; Kastner et al., 1998). A method of controlling lateral inhibition by neurons upstream was recently described in stimulus-sensitive areas, and was suggested to be a principal method also in higher cortical areas (Arevian et al., 2008).

We propose then that the task, and more exactly the representational precision required by the task, can top-down modulate the level of lateral inhibition in a salience map.

In this article, we directly investigate the influence of task demands on activation in such competitive interaction salience maps as a function of set size. We manipulate the attentional demands to investigate their effect on the activation curves in both model and data. For this purpose, we implemented the working memory model of Usher and Cohen (1999). We used different settings of the lateral inhibition parameter and derived predictions about the total activation in the map when the model was presented with different set sizes. Model predictions were then investigated with fMRI experiments, in which we manipulated attention to the items by varying the attentional demands needed to perform the task. In a first study, we implemented the model with a high and medium inhibition level. The predictions of the model with a high inhibition level were compared against the activation pattern found by Todd and Marois (2004), and the predictions of the model with the medium inhibition level were tested against the fMRI activation in the presumed salience map in an experiment where we used the task setting of Santens et al. (2010).

Study 1: Model

We simulated a computational model of a spatial working memory map and varied the inhibition parameter. We investigated whether we could replicate the results of Todd and Marois (2004) by implementing a high lateral inhibition factor, and then explored the model’s behavior with a medium level of lateral inhibition.

Methods

We used the model reported in Usher and Cohen (1999) because their model captures most of the critical features assigned to spatial working memory maps in the literature (Gottlieb and Goldberg, 1999; Vogel and Machizawa, 2004). Formally, this model belongs to the class of nonlinear leaky competing accumulation models for multiple-alternative choice paradigms (e.g. Bogacz et al., 2007). For easy reference we here report the model in detail also. A collection of 70 nodes was implemented, but similar results are obtained when different numbers of nodes (e.g., 80, 120) are used. Each node i has an activation value xi(t) at point time t. Each node received self-excitation with parameter (strength) α and lateral inhibition from all other nodes with parameter (strength) β (see Fig. 1 for graphical illustration). During presentation of a stimulus in the receptive field of a particular node i, an input of 1 was given to that node. In particular, activation xi(t) was governed by the equation:

\[ x_i(t) = -x_i(t-1) + \alpha F(x_i(t-1)) - \beta \sum_{j \neq i} F(x_j(t-1)) + I_i(t) + \text{noise} \]  

(A1)

where \( F(x) = 0 \) for \( x < 0 \) and \( F(x) = x/(1+x) \) otherwise. The function \( I_i(t) \) is an indicator equal to 1 if a stimulus is presented to neuron i at time t and 0 otherwise. Noise was sampled at each time step from a normal distribution with mean zero and standard deviation 0.05.

The parameter α was set at 4. For this first implementation, the parameter β was set either to 0.3 (high) or to 0.1 (medium). Items were presented to the models for five time steps; activation was then updated for another 45 time steps. Measured activation was integrated across the last five time steps. Fifty simulations were run; means and standard errors were calculated across these 50 simulations. As an illustration of how the activation is divided across the nodes, activation of all 70 nodes at the 50th time step is shown for the second simulation (medium inhibition) in Fig. 2A.
Although the model was not specifically set up as a spatial map, the principles underlying the model are the same as those used for spatial working memory maps in literature. Therefore, predictions for a spatial neural map can be derived from our simplified model. As argued in the introduction, the lateral inhibition parameter determines the threshold for neurons to become activated by input. With a high lateral inhibition parameter, the model removes all noise in the map, hence leading to a very precise representation in the map. We argue therefore that this situation will occur when very precise representations of the items are needed to solve the task. The situation with a medium inhibition parameter on the other hand will allow some noise in the map, hence leading to less precise representations. This can be seen more clearly in Fig. 2A where it is shown that for low numbers of items, items are correctly represented, but for higher numbers, some of the items are “lost” because of the competition. We argue that this situation will occur when the representation can be less precise to solve the task.

Results and discussion

With a high inhibition factor \( \beta = 0.3 \), the model predicts a close to linear increase in activation for set sizes 1 to 3 but then levels off for higher set sizes (see Fig. 3A). The predicted activation is in agreement with the fMRI data of Todd and Marois (2004; see also Todd and Marois, 2005; Kawasaki et al., 2008; Magen et al., 2009; Xu, 2009). In these studies, the items’ locations had to be precisely remembered and individuated. We proposed that this corresponds to the implementation with a high level of lateral inhibition. As predicted by the model, only a few items can be represented in this way, and the system reaches a capacity limit very soon.

Next, we implemented the model with a medium level of inhibition \( \beta = 0.1 \). As outlined in the introduction we expected the peak activation to occur at more than four items. Therefore we presented the model with higher set sizes (4, 8, 16, 32 and 64). The simulated activation curve first increased but then attained a peak activation (see Fig. 3B; see also Fig. 2A for a snapshot of the activity of one of the simulations). This peak activation limit was however at a much higher set size than with a higher lateral inhibition parameter \( \beta = 0.3 \). As the number of objects presented to the model increased above the peak activation, the activity in the map decreases in this case, leading to a nonmonotonous activation curve.

Study 1: fMRI experiment

We tested the predictions of the model with medium inhibition and large set sizes in an fMRI experiment. As argued above, the task used by Todd and Marois (2004) corresponds to a high inhibition parameter in the model because locations (actually, location/color conjunctions) have to be remembered very precisely. Therefore, we choose a task where all items need to be represented but memory representations can be less strict. The task of Santens et al. (2010) fulfills these requirements. Here, subjects are required to estimate the number of items (dots) presented, which obliges them to represent all items. However, no item
stimuli were divided in three categories (small, medium and large), which were controlled against one another. This procedure was described in detail elsewhere (Santens et al., 2010). Non-numerical parameters were divided in intensive parameters (individual item size and inter item spacing) and extensive parameters (accumulated area of all items in the display or total luminance, and total area spanned by the configuration) (Dehaene et al., 2005). Stimuli were constructed as triplets of dot patterns with increasing set size \( (n_{\text{small}} < n_{\text{medium}} < n_{\text{large}}) \) from now on referred to as \( n_s \), \( n_m \) and \( n_l \). The intensive parameters were constant between \( n_s \) and \( n_m \) and the intensive parameters were constant between \( n_m \) and \( n_l \). Therefore the intensive parameters covaried incongruently with increasing set size between \( n_s \) and \( n_m \), and the extensive parameters covaried congruently with increasing set size between \( n_m \) and \( n_l \). The intensive and extensive parameters were controlled in a reversed order compared to Santens et al. (2010). This was done because it allows a larger range of possible item sizes within the constraints of the control, especially for patterns with more items.

In order to make our stimuli more variable, we wanted to include more set sizes than three. Considering the estimation task, we wanted the task to be genuine estimation, rather than a categorization as small, medium and large set size. Therefore we used more set sizes (4, 8, 16, 32 and 64) than categories. Due to the implemented control for non-numerical parameters, this implies that individual set sizes could belong to multiple categories. Category \( n_l \) could be 4, 8 or 16 items, \( n_m \) could be 8, 16, or 32 items, and \( n_l \) could be 16, 32 or 64 items.

Displays were generated randomly by an adapted version of a Matlab program (Matlab 7.0.4, The MathWorks, Inc.) described in Dehaene et al. (2005). Items were displayed in an invisible circle which extended approximately 10 × 10 visual degrees around fixation point. The sample method for item size and total area spanned was the same as in Santens et al. (2010).

**Materials and methods**

**Participants**

Twenty-one adult male volunteers participated in this study and were paid for participation. One participant was excluded from all analyses due to self-reported motion during scanning. Five other participants were excluded due to poor performance on the task (see below). The remaining 15 participants were on average 24.1 ± 3.1 years old (range 18–30 years). All subjects were right-handed and had normal or corrected-to-normal vision. All subjects reported by means of a questionnaire having no neurological or psychiatric history, and gave written informed consent prior to scanning. The study was approved by the ethical committee of the Medical Department of Ghent University.

**Stimuli**

Stimuli were dot patterns with 4, 8, 16, 32 or 64 items. In order to remove confounding cues from non-numerical parameters, the specific information must be retained, making the task less strict and hence applicable to higher set sizes. It is noteworthy that the activation in the study of Santens et al. (2010) does not seem to reach a peak activation (set sizes 1 to 5), providing an indication that the capacity limit is higher in these task settings. Therefore, we used higher set sizes (4 to 64) in the present study. In order to make sure that subjects could perform the task, they were trained to reliably estimate the number of items before going into the scanner.

**Experimental procedure**

Before going into the scanner, participants were trained until they could reliably estimate the number of items. In a training block, each set size was presented six times, yielding training blocks of 30 trials. A trial in the training phase started with a fixation cross for 500 ms, followed by a display for 150 ms. Participants were asked to estimate the number of items in the display, and the answer was typed in by the experimenter. Feedback was given after every trial and at the end of each training block. Participants completed at least two training blocks, and had to reach a performance of 93% before they were allowed to participate in the fMRI experiment.

Following Santens et al. (2010), stimuli were presented for 150 ms in the fMRI experiment, white against a black background. A small yellow fixation cross remained on the screen throughout the whole experiment. Stimuli were presented on average every 5 s, with a jittering factor (Burck et al., 1998; Miezin et al., 2000) varying between 0 and 1600 ms, so that the interstimulus interval between two consecutive events could vary between 3400 and 6600 ms. Twenty percent of all events were null events. In order to make sure that subjects paid attention to the stimuli, occasionally (12 times per run) a task trial was introduced. In these task trials, two Arabic numbers were presented left and right of fixation and subjects were asked to indicate the number that corresponded to the set size of the previous display by pressing a button with their left or right index finger. The experiment consisted of five runs with 103 events per run. The order of the five event types \( (n_s, n_m, n_l, n_s, n_l, n_l) \) within runs (each trial type followed every other trial type equally often, Buckner et al., 1998). Order of displays with 4, 8, 16, 32 and 64 items was counterbalanced over all runs for each subject. The first trial was always a null event to improve the timing accuracy but was not used in the analysis.

**Fig. 3.** Activations for different set sizes presented to the model, with different inhibition factors \( \beta \). (A) \( \beta = 0.3 \); (B) \( \beta = 0.1 \); (C) \( \beta = 0.01 \).
At the end of the experiment, subjects were engaged in a short localizer experiment to determine human LIP, implemented as a block design run. This localizer was based on the finding that human LIP is involved in the preparation of eye movements (Corbetta et al., 1998; Baker et al., 2006). Stimuli for this run were single items with random position (within the invisible circle of 10 visual degrees) and random item size (between 0.2 and 0.63 visual degrees). Every stimulus was presented for 1 s, and immediately followed by another stimulus, yielding a dot which changed location and size every second. In the fcc condition, subjects were asked to make a saccade to the item and back to the fixation cross every time the item changed position. In the fixation condition subjects were asked to ignore the items and keep fixating the fixation cross. The task was indicated by the color of the fixation cross (red: make saccades, yellow: no saccades). Block duration was 16 s. The saccade and fixation blocks alternated and each block was repeated eight times.

The experimental procedure was controlled with E-Prime 1.1 SP3 (www.pstnet.com/eprime; Psychology Software Tools), running on an AMD Athlon 64 Processor (2.41 GHz) under Windows XP. Stimuli were presented through dual display MRI compatible LCD displays, mounted in a lightweight headset (resolution 800 × 600, refresh rate 60 Hz; VisuaStim XGA, Resonance technology Inc, http://www.mrvideocom/). An eye tracking system was mounted on the headset, and eye movements were monitored online by the experimenter. Eyemovement data were also recorded but were not sufficiently reliable for further processing.

Image processing and statistical analysis

Data analysis was performed with BrainVoyager QX 1.9 software package (Brain Innovation, Maastricht, The Netherlands; Goebel et al., 2006). Functional volumes were corrected for slice timing, motion package (Brain Innovation, Maastricht, The Netherlands; Goebel et al., 2006). Images were coregistered with the within-session anatomical volume. Anatomical data were corrected for inhomogeneity. Functional and high pass filtered (cutoff 0.0083 Hz) after linear trend removal. Anatomical data were corrected for inhomogeneity. Functional images were coregistered with the within-session anatomical volume for each run separately. Anatomical and functional volumes were then transformed into Talairach space. Functional images were smoothed with a Gaussian kernel of 8 mm FWHM prior to statistical analysis.

Functional data were subjected to GLM analyses with five predictors for the main experiment (n_0, n_0, n_0, response left, response right) or two predictors for the localizer run (saccade, no saccade) (protocol specified in milliseconds and convolved with a two Gamma hemodynamic response function, time to response peak = 5 s, time to undershoot peak = 15 s, response undershoot ratio = 0.6), for each run and each subject separately. For multi-subject GLM, runs of the same subject were implemented as fixed effects, between subjects as random effects. Activations are reported at the p-level stated in the text. Correction for multiple comparisons was implemented with a cluster-level corrected p-level of 0.05 (Forman et al., 1995). Conjunction analyses were calculated based on the minimum t-statistic compared against the conjunction null (Nichols et al., 2005).

Event-related average curves were plotted by extracting the mean medium attention load: whole brain analyses of the conjunction (n_0 < n_0) and (n_0 > n_0), thresholded at p < 0.01 with a cluster extent threshold of 239 voxels. Coordinates of the most activated voxel in the cluster are given in Table 1 and Fig. 4A. The reverse analysis (V-shaped activation curve) yielded no results.

These regions overlapped with the active regions in the working memory task of Todd and Marois (2004) in left posterior parietal cortex, and were only 14 mm removed from the centre of activation in right posterior parietal cortex. In comparison with Santens et al. (2010), our parietal regions were situated more inferior, 16 and 21 mm removed from the centre of activation on the left and right side respectively.

We calculated event-related averaging curves in the left and right parietal areas (multiple adjacent parietal activations in one hemisphere were taken together for this analysis) for each of the different set sizes (Fig. 4B). These curves show that the activation increased in both hemispheres from 4 to 8 items, but then dropped and remained constant from 16 items onwards. This is shown more clearly in Fig. 4C, in which we plotted the regression weights (beta values) from an

<table>
<thead>
<tr>
<th>Region</th>
<th>Coordinates</th>
<th>Voxels (n)</th>
<th>p-value</th>
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<td>Right parietal lobe</td>
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<td>3.94</td>
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<td>Left intraparietal sulcus</td>
<td>−30, −61, 37</td>
<td>3615</td>
<td>5.86</td>
</tr>
</tbody>
</table>

Table 1

Results of the fMRI experiment with medium attention load: whole brain analyses of the conjunction (n_0 < n_0) and (n_0 > n_0), thresholded at p < 0.01 with a cluster extent threshold of 239 voxels. Coordinates of the most activated voxel in the cluster are given in Talairach space. Voxels (n) report the number of active voxels in the clusters, resized to 1 × 1 × 1 mm voxels. t and p values are reported for the most active voxel in the cluster.
We performed a ROI analysis to test the activation pattern in the human homologue of monkey area LIP, as this region was previously found to house a salience map (Corbetta and Shulman, 2002; Connolly et al., 2002; Santens et al., 2010). For this purpose, the contrast saccade versus fixation was computed on the images of the localizer run, thresholded at \( p < 0.0005 \). Within the resulting activation network, we selected in both hemispheres a ROI which corresponded best with coordinates of human LIP as reported in the literature (Sereno et al., 2001; Simon et al., 2002; Koyama et al., 2004), which was then defined as a ROI for human LIP. The left hemisphere ROI comprised 3411 voxels (resized to \( 1 \times 1 \times 1 \) mm voxels) and was centered at \((-20, -64, 53)\); the right hemisphere ROI comprised 917 voxels and was centered at \((17, -62, 50)\). The ROIs exhibited only little overlap with the activations in the conjunction \((n_s < n_m)\) and \((n_m > n_l)\), but were situated more superior and anterior, and slightly more medial. Only the left hemisphere ROI overlapped with the most posterior and anterior end of the right hemisphere activation.

Next, the random effects analysis on the average activation over all voxels in these ROIs was computed for each contrast of the A-shape conjunction separately. This analysis was significant in the left hemisphere for both contrasts \([n_s < n_m]: t(14) = 2.11, p < 0.05; n_m > n_l]: t(14) = 3.07, p < 0.005\), rendering it significant for the conjunction based on the minimum \(t\)-statistic. In the right hemisphere, this was significant for the second contrast only \([n_s < n_m]: t(14) = -0.50, p = 0.62; n_m > n_l]: t(14) = 2.09, p < 0.05\).

**Discussion**

In this study, we investigated the activity of the salience map in a task setting with medium attentional demands (i.e. lower than in...
Todd and Marois, 2004). Furthermore, we investigated the activity of the salience map when presented with set sizes far above the capacity limit. We presented subjects with a large set size, and asked them to estimate the number of items. In this way, subjects were obliged to represent all items in the display, as concentrating on only a few would yield incorrect results.

In the fMRI analysis, the pattern of activity predicted by the model was indeed found in areas comparable with areas previously identified in working memory paradigms (Todd and Marois, 2004; Santens et al., 2010). The same pattern of activation was also found in the human homologue of LIP, the area traditionally connected with a salience map. More specifically, we found an increasing activation up to eight items, but activity decreased significantly for larger set size.

Study 2: Model

In this study, we investigated a model implemented with a low inhibition factor. In our model, which used the same principles as models for spatial neural maps in the literature, low lateral inhibition effectively lowers the threshold for neurons to become activated. This means that random noise fluctuations can activate neurons. This leads to a much coarser representation of the items in the spatial map (see Fig. 2B for an illustration). We propose therefore that low inhibition is implemented when the representation of the items does not have to be precise. This was then tested in an fMRI experiment with low attentional demands.

Methods

The inhibition parameter β was now set to 0.01 (low inhibition). The model was again shown 4, 8, 16, 32 and 64 items.

Results and discussion

The output of this model is shown in Fig. 3C, and shows a V-shaped activation curve. The fact that the activation for the small set sizes is higher than for larger set sizes can be explained as follows: Because of random noise, the activation of each node is above zero. When only a few objects are presented, the activated neurons are not capable of suppressing the noise activation in the other nodes because the inhibition parameter is low. When the set size increases, the inhibition they can exert together increases, and they are now able to inhibit the noise activation, which results in less activation in the map as a whole. When the set size increases further, the activation will now increase with the number of objects presented. It is noteworthy that the model does not seem to reach a peak activation, even for the highest set size (64) presented. See Fig. 2B for an illustration of how the activity is divided across the nodes in one of the simulations.

Study 2: fMRI experiment

The predictions of the model were again tested in an fMRI experiment. This experiment was exactly the same as the first fMRI experiment, with the exception of the task. In this case, we chose a task in which the representation of the items in the salience map need not be precise, that is, a task where attentional demands are extremely low.

Materials and methods

Participants

Twenty-one adult male volunteers participated in this study and were paid for participation. One participant was excluded from all analyses because he admitted afterwards to suffer from claustrophobia. Another participant was excluded because he missed a considerable number of all task trials. The remaining 19 subjects were on average 20.7 ± 2.6 years old (range 18–28 years). All subjects were right handed and had normal or corrected-to-normal vision. All subjects reported by means of a questionnaire having no neurological or psychiatric history, and gave written informed consent prior to scanning. None of the participants had participated in the fMRI experiment of Study 1.

Stimuli and experimental procedure

Stimuli and the experimental procedure were the same as in Study 1, with the exception that the subjects were not trained before participating in the scan session, as the task did not require a precise representation of objects. The task was the only difference with Study 1. Instead of asking subjects to report the number of items in the previously presented display, we now presented occasionally a ‘doubled’ display. In these trials, the same pattern was shown twice, left and right of the fixation cross. Subjects were merely asked to detect this by pressing one of two response buttons. Subjects were encouraged to use both response buttons at random.

It is important to note that here, as in Study 1, the task was implemented in separate task trials, which were not included in the analysis. Furthermore, the task trials were only sporadically and, more importantly, unpredictably implemented. Therefore, the subjects were required to analyze each stimulus, because each stimulus could be followed by a task trial. We took care that in both tasks, the whole stimulus had to be analyzed in order to solve the task. However, the task in the medium-attention experiment (estimation; Study 1) required a much more detailed analysis of the stimulus than the low-attention task (pattern recognition; Study 2). We therefore argue that the only difference between the two experiments is the attention to be directed to the stimuli in order to solve a possible task trial.

At the end of the experiment, subjects were engaged in a short localization experiment to determine ROIs of human LIP.

Imaging procedure, image processing and statistical analysis

These were the same as in Study 1.

Results

Behavioral results

Again, the behavioral results were only analyzed to ensure that the participants were attentively processing the stimuli. One subject missed 13.3% of the task trials and was excluded from further analysis.

Whole brain analysis

We tested the prediction of the model that the activation in this task setting would yield a V-shaped curve. This was tested with the conjunction \((n_{i_0}>n_{i})\) and \((n_{i_0}<n_{i})\). This analysis, at a \(p\)-level of 0.005 with a cluster threshold of 190 voxels, revealed three clusters (see Fig. 5A). A small cluster was situated in the inferior frontal gyrus, and two large clusters were situated bilateral in the superior parietal lobe. The reversed analysis (a \(\Lambda\)-shape activation) yielded no results. See Table 2.

The regions found by Todd and Marois (2004) in a working memory paradigm overlapped with our posterior parietal region in the left hemisphere. In the right hemisphere our posterior parietal regions were situated slightly more lateral than those of Todd and Marois (2004), but the distance to the centre was only 9.4 mm. The regions of Santens et al. (2010) overlapped with the medial part of the left posterior parietal region. In the right hemisphere our posterior parietal regions were situated more inferior, centre to centre distance was 20 mm.

The event related averaging curves were calculated for each set size separately in both parietal regions (Fig. 5B). These curves show that there is a decrease from four items to eight items, which then turns into an increase from eight items onwards. This pattern was
confirmed by the regression weights (beta values) of an analysis where we specified events in terms of set size (Fig. 5C). From this graph it is clear that the activation takes the form of a V-shape with a dip between 8 and 16 items.

**ROI analysis**

The activation pattern was again tested in the human LIP region. The ROIs of the human LIP region were determined in the same manner as in Study 1, based on the images of the localizer run which was again measured at the end of the experiment. The left hemisphere ROI comprised 1316 voxels and was centered at (−21, −60, 57); the right hemisphere ROI comprised 2066 voxels and was centered at (18, −63, 54). The ROIs were situated more medial and superior than the activations of the conjunction, but overlapped partly in the left hemisphere.

The random effects analysis on the average activation over all voxels in these ROIs was computed for each contrast of the V-shape conjunction separately. This analysis was significant for all contrasts in both hemispheres [left: \( n_s > n_m \): \( t(18) = 2.46, p < 0.02 \); \( n_m < n_l \): \( t(18) = 2.33, p < 0.02 \); right: \( n_s > n_m \): \( t(18) = 2.90, p < 0.005 \); \( n_m < n_l \): \( t(18) = 2.32, p < 0.02 \)], rendering the conjunction based on the minimum \( t \)-statistic significant in both hemispheres. This analysis

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Table 2

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<th>Region</th>
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</tbody>
</table>
revealed that our task caused activation predicted by our working memory model in regions previously shown to house a salience map.

Comparison with Study 1

We compared the activations found in the two fMRI experiments. In the left hemisphere, the activations found in Study 2 were situated slightly more anterior than the activations found in the Study 1. There was however considerable overlap (see Fig. 5A). The overlap was centered around coordinates (−25, −64, 40) and comprised 374 voxels.

In the right hemisphere, the activations found in Study 1 were situated in the same region, but extended more anteriorly. The overlap was situated around (27, −64, 34) and comprised 72 voxels (see Fig. 5A).

Discussion

We tested the prediction that the activation pattern for different set sizes would change with a different task setting. More specifically, we predicted that the activation pattern would display a V-shaped curve when the task did not require a precise representation of the items in the display. This pattern was confirmed. The conjunction analysis which tested V-shape activation yielded significant clusters in the left and right posterior parietal lobe. The ROI analysis for the same contrasts in human LIP was also significant.

Inspecting the pattern for the different set sizes revealed a small decrease from 4 to 8 items, which turned in an increase from 8 or 16 items onwards.

It could be noted that the decrease for smaller set sizes is larger in the fMRI data than in the model data. Rather than fine tuning the parameters in our model to precisely fit the data, we choose to ignore quantitative differences and concentrate on qualitative differences. Therefore, we only compared the form of the curve predicted by the model (V-shape) with the fMRI data, but we were not interested in the exact value of the minimum in the curve.

General discussion

In two experiments, we found evidence for salience maps in the human brain, based on competitive interactions as proposed in computational cognitive models. In Study 1, when the level of lateral inhibition in the model was of medium height, the activation curves across large set sizes (4 to 64) exhibited a Λ-shaped curve. Correspondingly, when subjects were required to deploy a medium level of attention to the individual items, the activation curves in IPS were Λ-shaped as well. In Study 2, when the level of lateral inhibition in the model was low, the activation curve of the model was V-shaped. Consistent with this, when subjects were not required to deploy much attention to the items in the displays, the activation curves in that same IPS region were V-shaped. Earlier authors already observed nonmonotonous load response functions with set sizes up to 7 (Linden et al., 2003; Magen et al., 2009). The present paper goes beyond these earlier studies by empirically investigating much larger set sizes and by proposing a computational framework that predicts these nonmonotonocities.

The idea that the amount of lateral inhibition in the salience map is task-dependent suggests that the level of lateral inhibition is top-down regulated. It is likely that this top-down modulation originates in frontal cortex, as this area is generally thought to represent current task instructions (e.g. Brass and von Cramon, 2004). A similar notion was proposed by Edin et al. (2007). These authors argued that dorsolateral prefrontal cortex modulates the capacity limit of the salience map in parietal cortex by injecting a constant level of input to all neurons in the map. Although in their model the level of lateral inhibition was not directly modulated, they proposed that different levels of input from the dorsolateral prefrontal cortex lead to different capacity limits of the salience map. Further, Rolls and Deco (2006) proposed that dorsolateral prefrontal cortex selectively biases particular locations in salience maps in parietal cortex. Hence, top down attention from frontal areas to parietal salience maps may be implemented with different mechanisms. In general though, all these proposals are consistent with a biased competition framework in which frontal areas influence competitive interactions in upstream areas depending on different contextual factors (e.g. task demands; Desimone and Duncan, 1995).

We argued that the inhibition parameter determines the representational precision of the items in the salience map, which determines the level of attention directed to individual items. Consequently, different levels of the inhibition parameter may correspond to the two modes of attention described by Treisman (2006) and Treisman and Gelade (1980). One mode described by Treisman is focused attention, in which attention is directed to a small region in visual space and to the features of the objects in that small region. This mode may correspond to a very high inhibition parameter, in which only few (or possibly even a single one) locations are attended. The second mode described by Treisman is broad attention, in which attention is spread across many locations (possibly the whole visual field). This mode is useful for extracting general information such as texture or color of the visual scene. We propose that this second mode corresponds to a competitive interaction model with a low inhibition parameter in which many locations are simultaneously active. It must be noted though that our model does not subscribe to a fixed two-mode system as proposed by Treisman. Instead, it allows a continuous range of attentional modes dependent on current task demands, and implemented by different inhibition parameter values.

Earlier papers on spatial attention and visual working memory have contrasted the “fixed slots” concept with an approach where activation can be dynamically allocated across multiple spatial locations (e.g. Bays and Husain, 2008; Zhang and Luck, 2008). In the computational cognitive neuroscience literature (e.g. Deco and Rolls, 2005; Itti and Koch, 2000; Rolls and Deco, 2006; Usher and Cohen, 1999), attention has instead been considered to emerge from competitive interactions between different neurons and neural layers. Although this competitive interaction viewpoint has similarities to the other two approaches, the present data strongly favor the former. It is worth noting however that this finding was only possible via a close interaction between modeling and imaging work. For evaluating theories on the functioning of a highly nonlinear system such as the human brain, we consider such an interactive approach to be a major asset.

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